

# Reconstructing biological invasions using public surveys: a new approach to retrospectively assess spatio-temporal changes in invasive spread

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Received: 7 February 2018 / Accepted: 31 August 2018 / Published online: 14 September 2018  
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**Abstract** Management of biological invasions increasingly relies on the knowledge of invasive species' dispersal pathways that operate during introduction and post-introduction dispersal. However, the early stages of biological invasions (introduction, establishment, and initial spread) are usually poorly documented, limiting our understanding of post-introduction dispersal and the role of humans in invasive spread. We aim to assess a new approach to retrospectively understand spatio-temporal patterns of introduction, establishment, dispersal, and spread in biological invasions, using the case study of an ongoing invasion of the Indian bullfrog (*Hoplobatrachus tigerinus*) on the Andaman archipelago, Bay of Bengal. We sampled 91 villages on eight human inhabited islands of the Andaman archipelago from 2015 to 2016. We assessed the occurrence of the

bullfrog using visual encounter surveys and recorded the invasion history (year of establishment, source site, and dispersal pathway) for each site by surveying 892 key informants (farmers, plantation workers, and aqua-culturists). We sought to corroborate the reconstructed invasion history with false positive occupancy modelling, using site specific covariates that corresponded to hypotheses on specific dispersal pathways. The bullfrog occurred in at least 62% of the sampled sites spread over six islands, a dramatic increase to the previously known invaded range. The bullfrog was most likely introduced in early 2000s, and its exponential expansion has occurred since 2009. 'Contaminants' of fish culture trade and intentional 'release' were reported to be the primary pathways of introduction and post-introduction dispersal, facilitating introductions from the Indian mainland and inter-island transfers. False-positive occupancy modelling confirmed that three sites on the archipelago influenced the invasion disproportionately by acting as dispersal hubs. The study elucidates the efficacy of using public surveys to identify dispersal pathways and hubs, and to understand invasive spread, when such information is typically unavailable otherwise. The proposed approach is scalable to other systems and species.

**Electronic supplementary material** The online version of this article (<https://doi.org/10.1007/s10530-018-1839-4>) contains supplementary material, which is available to authorized users.

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**Keywords** Amphibia · Andaman Islands · Dispersal pathway · False positive · *Hoplobatrachus tigerinus* · Key informant survey

## Introduction

The role of humans in species dispersal is of interest to both conservation biology and invasion biology (Trakhtenbrot et al. 2005). With globally accelerating rates of biological invasions (Seebens et al. 2017) and their consequent negative impacts (Simberloff et al. 2013), it is imperative to understand the processes governing human mediated introduction of species and subsequent dispersal within their non-native range (Hulme 2009; Wilson et al. 2009). The success of risk assessment, biosecurity, early detection, eradication and control actions depend on the knowledge of invasive species dispersal pathways (Hulme 2015; Essl et al. 2015; Pergl et al. 2017). Acknowledging this, global and regional strategies aiming to manage invasions now aim to identify, prioritize, and manage human mediated introduction and dispersal pathways (CBD 2014; Genovesi et al. 2015).

The early stages of invasions (e.g. introduction, establishment, and initial spread) are often not well documented (Puth and Post 2005) in comparison to the latter stage of invasive dominance, where impacts often become apparent (Blackburn et al. 2011), and in turn generate research attention. As an invasion progresses towards the latter stages, information regarding spatio-temporal patterns of distribution and dispersal in the early stages may be lost. This is particularly relevant for invasions resulting from accidental dispersal pathways. Nevertheless, understanding the processes leading up to exponential invasive spread could lead to better management of potential new invasions. To this end, several approaches have been formulated to study invasions retrospectively, relying on genetic tools (Fitzpatrick et al. 2012), individual based models (Vimercati et al. 2017), herbarium/museum specimens (Loo et al. 2007), and more frequently on published or unpublished ‘first observation’ records (Zhulidov et al. 2010; Nunes et al. 2015; Horvitz et al. 2017). However, there are limitations to each of these approaches. Although genetic information can help determine source populations, it may have limited power to elucidate invasion history (see Barun et al. 2013); individual based models may be highly data intensive; museum/herbarium records and literature may be subject to bias (e.g. taxonomic or sampling bias, McGeoch et al. 2012; or bias in time of collection and detection, Aikio et al. 2010). New approaches such as geographic

profiling can provide leads on likely source populations using sightings of the species by various sources (including passive observations by members of the public, Faulkner et al. 2016). Historical ecology is also seen as a potential window to understand the spatio-temporal dynamics of long-term invasions (Clavero and Villero 2013; Van Sittert and Measey 2016).

Public surveys have been used in invasion science to assess distribution (Goldstein et al. 2014; Crall et al. 2015), public attitude towards management (Bremner and Park 2007), risk assessment (Chown et al. 2012), and the ability of the public to identify invasive species (Somaweera et al. 2010). Li et al. (2011) determine residence time of invasive American bullfrogs *Lithobates catesbeianus* in 65 water bodies using interviews of local residents, albeit with a small sample size (1–3 interviews per site). Positive public perception may lead to intentional introductions (e.g. the introduction of “pretty” plants as ornamentals, Reichard and White 2001 or “cute” animals as pets, Kikillus et al. 2012) and negative perception may lead to voluntary management (Somaweera et al. 2010). Assessing this perception is also essential for management in human inhabited landscapes (Sharp et al. 2011).

Public surveys can be a potential tool to reconstruct invasion history but should be corroborated with field observations to ensure reliability. False-positive occupancy modelling can incorporate both field observations and key informant data (Miller et al. 2011; Pillay et al. 2014; Chambert et al. 2015) and can be applied to reliably and rapidly estimate distributions of invasive species (Mohanty et al. 2018). In the present study, we combine key informant and visual encounter surveys using multi-method false positive occupancy models (Miller et al. 2011; Mohanty et al. 2018), such that the visual encounter surveys are used to validate key informant responses on both detection/non-detection and spatial information on the invasion.

We explore this approach with the case study of an anuran amphibian invasion on the Andaman Islands, Bay of Bengal. In doing so, we also aim to contribute to the relatively understudied subject of amphibian invasions (Pyšek et al. 2008), which have considerable impact on native biodiversity (Kraus 2015), comparable to that of invasive freshwater fish and birds (Measey et al. 2016). Common introduction pathways (and probable post-introduction dispersal pathways) in amphibians are cargo and the nursery trade, along with

intentional pet trade and culture for human consumption (Kraus 2007). Although studies on amphibian invasions have increased noticeably in the last decade, three species (the cane toad *Rhinella marina*, the American bullfrog *Lithobates catesbeianus*, and the African clawed frog *Xenopus laevis*) account for nearly 80% of published research; knowledge on dispersal is lacking for most amphibian invasions.

The invasion of the Indian bullfrog *Hoplobatrachus tigerinus* on the Andaman Islands was reported recently (Harikrishnan and Vasudevan 2013), identifying an introduction in 2009–2010 from the Indian mainland. This large ranoid frog is expected to have impacts, through predation and competition, on small vertebrates of the Andaman archipelago (Mohanty and Measey 2018). In this study, we aimed to assess our novel approach to reconstruct spatio-temporal patterns of introduction, establishment, dispersal, and spread using the case study of the ongoing invasion of the Indian bullfrog. We aimed to (i) assess the current distribution of the invasive bullfrog population on the Andaman archipelago using a combination of key informant surveys and field surveys, (ii) determine its introduction and post-introduction dispersal pathways based on key informant surveys, and (iii) assess temporal changes in distribution and dispersal using both key informant surveys and field surveys. In addition, we evaluate the public perception of the species in the local community. We use this case study to explore the use of public surveys as a complementary tool in generating invasion history, especially for dispersal and spread.

## Methods

### Study species

The Indian bullfrog, *Hoplobatrachus tigerinus* (Daudin 1802), has its native range on the Indian sub-continent encompassing low to moderate elevations in Nepal, Bhutan, Myanmar, Bangladesh, India, Pakistan, and Afghanistan (Dutta 1997). This large bodied frog (up to 160 mm) has high reproductive potential (up to 5750 eggs per clutch, once per year; Oliveira et al. 2017) and is uncommon or absent in forested and coastal regions, but occurs as a human commensal (Daniels 2005). The bullfrog has been introduced to Madagascar (Glaw and Vences 2007), and possibly to

the Maldives (Dutta 1997) and Laccadive Islands (Gardiner 1906). It was reported to occur in two sites on Middle Andaman and South Andaman Island (Webi and Wandoor; Harikrishnan and Vasudevan 2013), followed by observations on Havelock and Neil islands (Rangaswamy et al. 2014). Intentional human-assisted dispersal reportedly occurred within the Andaman archipelago, along with confirmed establishment in at least two locations, indicating the beginning of an invasion (Harikrishnan and Vasudevan 2013). Since these initial reports, no systematic studies have been carried out on the bullfrog invasion and there is a lack of critical information on distribution and dispersal of the species on the Andaman Islands. Moreover, museum specimens and citizen science records are unavailable.

### Study area

The Andaman Islands, in the Bay of Bengal, are situated 1200 km to the east of the Indian mainland, ranging from 10°30'N to 13°40'N, and from 92°10'E to 93°10'E. This tropical island group, comprising of ca. 300 islands, is part of the Indo-Burma global biodiversity hotspot (Myers et al. 2000). The majority of the landmass is accounted for by eight islands with major human habitations (Table 1) and the mostly uninhabited Interview and Rutland islands (Forest Statistics 2013). Primary and secondary forests encompass nearly 87% of the entire archipelago, falling under several protection regimes of Protected Areas and Tribal Reserves (Forest Statistics 2013). Roughly 40% of the reptiles and amphibians ( $n = 53$ ) are endemic to the Islands (Harikrishnan et al. 2010). Several introduced invertebrates and vertebrates also occur, including fishes, mammals, birds and reptiles (Mohanraj et al. 1997; Rajan and Pramod 2013); the Indian bullfrog was the first non-native amphibian to be reported (Harikrishnan and Vasudevan 2013). The human population on the archipelago is approximately 344,000 people (Directorate of Economics and Statistics 2013), distributed across the eight islands with major human habitations; settlements are mostly comprised of villages along with one or more towns on each island. Agriculture and aquaculture (subsistence and commercial) are widely practised in the archipelago; most villages have artificial ponds for aquaculture and sustenance.

**Table 1** Sampling effort for key informant surveys and visual encounter surveys on the Indian bullfrog *Hoplobatrachus tigerinus*, at 91 sites on eight human inhabited islands of the Andaman archipelago, from 2015 to 2016

Island	Size (km <sup>2</sup> )	Sites	Respondents/site (SD)	Sites with field survey	Sites detected
North Andaman	1375.99	29	9.66 (1.54)	27	23
Middle Andaman	1535.5	27	10.19 (1.11)	27	26
Long	17.9	1	7	0	–
Baratang	297.6	5	9 (2.35)	4	0
Havelock	113.93	5	10.8 (1.79)	5	5
Neil	18.9	2	10.5 (0.71)	2	2
South Andaman	1348.2	13	9.62 (1.26)	13	1
Little Andaman	734.39	9	9.44 (1.13)	6	0

### Study design

The reconstruction approach involves three key components: (i) false-positive occupancy modelling of current invasive distribution using key informant and visual encounter surveys, (ii) generating information on ‘time of establishment’ (and consequently spread rate) and dispersal pathways from only key informant surveys, and (iii) using spatial information (‘source sites’) obtained from key informant surveys in false-positive occupancy models to corroborate key informant data with field observations.

The first report of the bullfrog on the Andaman Islands described populations occurring in two villages of Middle and South Andaman Islands (Harikrishnan and Vasudevan 2013), and no occurrence on uninhabited islands (Rangaswamy et al. 2014; Harikrishnan and Vasudevan 2015). Given the synanthropic nature of the species (Daniels 2005), we assume that the bullfrog would most likely occur in human-modified areas if they were present in a region. For example, if a region containing the bullfrog encompasses forests and adjoining villages, we assume that individuals will at least be present in the villages. Under this assumption, we defined a village with natural boundaries (forests, and not administrative boundaries) as the observational unit to sample for occurrence and invasion history. This strategy was further informed by the probable intentional dispersal of the bullfrog, from one village to another, in the region (Harikrishnan and Vasudevan 2013). We identified 101 villages on the archipelago, but we were unable to sample in ten villages due to poor

accessibility. Overall, we sampled 91 villages on eight human inhabited islands of the archipelago from 2015 to 2016. Sampling consisted of two components: (i) visual encounter surveys to determine occurrence and (ii) key informant surveys to generate invasion history.

Two personnel carried out visual encounter surveys in the evenings (starting any time between 1800 and 2000 h), searching for bullfrogs near water bodies, agricultural fields, and plantations (preferred habitats; Daniels 2005). In those cases where bullfrogs were not detected on the first survey, we sampled again on a second evening. The survey ended upon confirming presence or continued for a minimum of 1 h. We could carry out visual encounter surveys in 84 villages (92% of total; Table 1), due to logistical constraints of sampling in the evening at certain locations.

We conducted 892 key informant surveys in all 91 selected villages (with an average of ca. 9.8 participants (SD = 1.38, range 4–15) per village; Table 1). Our aim was to survey ten respondents per site (given that most villages are small with 50–100 households) in order to attain convergence in responses. Key informants were defined as farmers, plantation workers, and aqua-culturists, i.e. those who engage with outdoor work on a daily basis and are likely to encounter the target species. We found and selected key informants by searching for people working in ponds, agricultural fields, and plantations or by enquiring for their profession on visiting their household. We conducted surveys individually and attempted to cover most areas of a village, in order to avoid clustered samples. The surveys aimed to

obtain information on bullfrog occurrence, invasion history (e.g. time of first observation, vector and source of introduction/post-introduction dispersal), and *perception* of the species (e.g. beneficial, harmful; Appendix 1 in electronic supplementary material) for each site. To avoid cross-contamination of responses, we sought answers only regarding the village of the respondent. When participants provided information on the introduction of bullfrogs through intentional release, we attempted to follow up with the personnel involved in the actual introduction to gather further details. The median age of the participants was 42 (17–85); the survey included 123 females (14%) and 18 anonymous respondents, which reflected the existing gender bias of the categories of key informants targeted. The surveys were a combination of structured and semi-structured questions and carried out in the local languages (Hindi, Bengali, and Tamil). We showed respondents photographs of the Indian bullfrog (adult) to assist with the question ‘Have you sighted this frog in this particular village?’ (Appendix 1 in electronic supplementary material). Verification was carried out based on the local name, morphological features, and behaviour in order to avoid species misidentification. As the bullfrog’s large body size, greenish-brown colouration, and guttural vocalizations are markedly different from that of native frogs, respondents were provided further information to aid in identification, only upon request.

### Data analysis

For analyses on invasion history, we did not include sites with only one report of presence by key informants ( $n = 4$ ), to reduce uncertainty. We also did not consider responses where the participant answered a question with a rider of ‘uncertain’. We generated invasion history for each site from key informant surveys with respect to time of first observation, introduction/dispersal vector, and source site, by obtaining modal responses to each corresponding question (Appendix 1 in electronic supplementary material). We considered the modal value (instead of the average; Li et al. 2011) of first observations per site to indicate time of establishment of the bullfrog in that site. Based on the time of establishment, we assigned each site to one of five time periods, each of three years duration (i.e. 2001–2003, 2004–2006, 2007–2009, 2010–2012, and

2013–2015). We evaluated the increase in the number of sites with bullfrogs, across the five time periods, using linear, exponential, and logistic growth curves.

Information on introduction/dispersal vector and source site were classified as ‘uncertain’ if more than 50% of the respondents did not answer the question on introduction/dispersal vector (Fig. 3). As the question on source site was nested within introduction/dispersal vector, the proportion of respondents for each question was analysed step-wise. We also extracted independent introduction events from public surveys by considering the reported source site and recipient site, and the reported personnel involved; this information was validated with the actual personnel who carried out the introduction. We analysed the responses on perception toward the bullfrog by considering each response as an individual datum; we compared responses across two time periods signifying relatively old (2001–2009) and new invasions (2010 onwards) using a Wilcoxon signed rank test in the statistical software R 3.4.1 (R Core Team 2017). Even though, two questions regarding the perception were semi-structured, we categorized similar responses *post hoc*. All GIS based analyses were carried out on ArcGIS 10.3.1 (ESRI 2012).

We constructed occupancy models to estimate site-specific occupancy and to test for the likelihood of potential dispersal pathways. Following Mohanty et al. (2018), we addressed the possibility of false positive detections in the public surveys using multi-method false positive occupancy models (Miller et al. 2011) along with the standard McKenzie models (MacKenzie et al. 2002), in the program PRESENCE 6.4 (Hines 2010). We built a detection/non-detection matrix consisting of both key informant observations (uncertain data) and one field observation (certain data) per site. All detection/non-detection observations used for the occupancy models belonged to the same time period (2015–2016). For false-positive models, we assumed that ‘certain data’ did not contain false-positives. To model this assumption, we fixed the parameter ‘ $b$ ’ (probability that a detection is classified as certain when the site is occupied, and the species is detected) for all occasions to 0; ‘ $P_{10}$ ’ (probability of detecting the species at a site when the site is unoccupied) was fixed to 0 only for field observations. We did not estimate differential true-positive detection probability ( $P_{11}$ ) for key informant and field surveys, as we did not carry out multiple field surveys



of the same site. We estimated occupancy rate ( $\psi$ ), true-positive probability, false-positive probability, and associated 95% confidence intervals.

We included seven site specific covariates in the models, representing dispersal pathways (*sensu* Hulme et al. 2008), to model occupancy; the covariates included distances to the nearest port (*stowaway in shipping*), major road (*stowaway in transport and unaided*), town (*stowaway in trade*), and three ‘dispersal hubs’, individually and together (local influence through any dispersal pathway). A ‘dispersal hub’ (see “Results” section) was defined as a site that served as the origin of multiple dispersals in the invaded range, based on the reported source (modal response) of each site. Dispersal hubs were defined to be distinct from ‘introduction hubs’, which were defined as sites with multiple introductions originating from them, located outside the invaded range of the Andaman archipelago. In all, we built 16 candidate models and used the Akaike information criterion (AIC, Burnham and Anderson 2002) to select suitable models.

## Results

From visual encounter surveys (2015–2016), we detected the Indian bullfrog in 57 villages, located on five of the eight sampled islands, with no detections obtained from Baratang, Long, and Little Andaman Islands (Table 1). A new population of Indian bullfrog was observed on Little Andaman Island in 2018. Of the 16 candidate models, the false positive multi-method model with the covariate ‘distance to nearest dispersal hub’ was chosen as the most suitable (Table 2). Site-specific occupancy estimates were higher on North and Middle Andaman as compared to Neil, Havelock, and South Andaman Islands (Fig. 1). Models which accounted for false positive detection performed better in terms of AIC, although the overall occupancy rate overlapped between the standard constant detection model and the standard false positive model (Table 2). The best model estimated a true positive detection probability ( $P_{11}$ ) of 0.93 (0.90–0.95) and a false positive detection probability ( $P_{10}$ ) of 0.04 (0.02–0.08; Table 2).

Respondents reported presence of the bullfrog on the Andaman archipelago as far back as 2000–2001, and establishment in seven sites up to 2009. A further 29 sites were reported from 2010 to 2012, and another

23 sites from 2013 to 2015 (Figs. 2, 3). An exponential curve ( $R^2 = 0.77$ ,  $y = 0.47e^{0.83x}$ ) best fitted the increase of sites with bullfrogs over the five time periods. Contamination of fish stocks with bullfrog propagules (eggs and tadpoles; hereafter ‘fish culture’) was reported to be a major mode of introduction and post-introduction dispersal within the archipelago. Intentional capture-release of post-metamorphic individuals (hereafter, ‘release’) was reported to operate only as a major mode of post-introduction dispersal (Figs. 2, 3). Post-introduction, natural dispersal through flood-waters and stowaways in transport of cargo was also mentioned. Fish culture was reported in more sites than release, which was only noted in sites post 2009 (Figs. 2, 3). Respondents suggested that private traders were the source of fish stocks from the Indian mainland, as well as the Department of Fisheries, and local self-government organizations (*Panchayat*).

The public surveys detected 17 independent releases to 14 sites (Fig. 3), from a total of 38 responses. The release events moved the bullfrog over an average distance of 47.48 km (SE = 11.81, range 6.2–188 km). The stated purpose behind five such releases was consumption (3 events, including one escape) and novelty (2 events), while information about the others were unavailable. We recorded release events in four sites where the majority of respondents claimed fish culture as the source.

‘Introduction hubs’ included West Bengal and unidentified locations on the Indian mainland and were reported for the fish culture pathway only. We identified three ‘dispersal hubs’ on the Andaman archipelago–Billyground–Nimbudera cluster, Diglipur, and Webi (Fig. 3); Webi was reportedly associated with the release pathway, while the remaining two sites acted as sources of both the fish culture and release pathways. Based on the selected occupancy model (Table 2), villages nearer to any of the dispersal hubs had higher site specific-occupancy as compared to sites farther from the hubs (Fig. 1).

The majority of respondents reported only negative impacts of the bullfrog, followed by those who reported both negative impacts and benefits, those who were neutral, and finally those who only reported benefits (Fig. 4). Perception of respondents was not found to differ in sites with old and new invasions ( $V \sim 0$ ,  $p = 0.99$ ; Fig. 4). The most frequently reported negative impact was that the bullfrog preys

**Table 2** Models explaining the occurrence of the Indian bullfrog *Hoplobatrachus tigerinus* at 91 sites on the Andaman archipelago, with estimates of occupancy ( $\psi$ ), true positive detection probability, and false positive detection probability along with 95% confidence intervals

Model	AIC	Occupancy ( $\psi$ )	True-positive ( $p_{11}$ )	False-positive ( $p_{10}$ )
psi(source), p(.), p <sub>10</sub> (.), b(.)*	507.71	Site-specific	0.93 (0.90–0.95)	0.04 (0.02–0.08)
psi(Webi), p(.), p <sub>10</sub> (.), b(.)	512.11	Site-specific	0.93 (0.91–0.95)	0.04 (0.03–0.08)
psi(Diglipur), p(.), p <sub>10</sub> (.), b(.)	513.54	Site-specific	0.93 (0.90–0.95)	0.04 (0.02–0.08)
psi(BG-ND), p(.), p <sub>10</sub> (.), b(.)	514.41	Site-specific	0.93 (0.91–0.95)	0.04 (0.03–0.08)
psi(port), p(.), p <sub>10</sub> (.), b(.)	551.66	Site-specific	0.93 (0.91–0.95)	0.04 (0.03–0.07)
psi(town), p(.), p <sub>10</sub> (.), b(.)	551.66	Site-specific	0.93 (0.91–0.95)	0.04 (0.03–0.07)
psi(.), p(.), p <sub>10</sub> (.), b(.)	554.01	0.63 (0.52–0.72)	0.93 (0.91–0.95)	0.04 (0.03–0.08)
psi(road), p(.), p <sub>10</sub> (.), b(.)	582.75	Site-specific	0.92 (0.89–0.94)	0.04 (0.03–0.08)
psi(source), p(.)	705.23	Site-specific	0.84(0.81–0.87)	–
psi(Diglipur), p(.)	705.54	Site-specific	0.84(0.81–0.87)	–
psi(Webi), p(.)	706.71	Site-specific	0.84(0.81–0.87)	–
psi(BG-ND), p(.)	709.98	Site-specific	0.84(0.81–0.87)	–
psi(.), p(.)	720.03	0.71 (0.61–0.80)	0.84(0.81–0.87)	–
psi(port), p(.)	728.95	Site-specific	0.84 (0.81–0.87)	–
psi(town), p(.)	728.97	Site-specific	0.84 (0.81–0.87)	–
psi(road), p(.)	749.84	Site-specific	0.83 (0.80–0.86)	–

Site-specific covariates include distance to nearest—port, town, major road, three dispersal hubs individually and in combination. Dispersal hubs are defined as source sites for more than one inter-island introduction and include BG-ND (Billyground-Nimbudera cluster), Webi, and Diglipur; ‘source’ denotes distance to nearest dispersal hub

\*b—Probability that a detection is classified as certain when the site is occupied and the species is detected

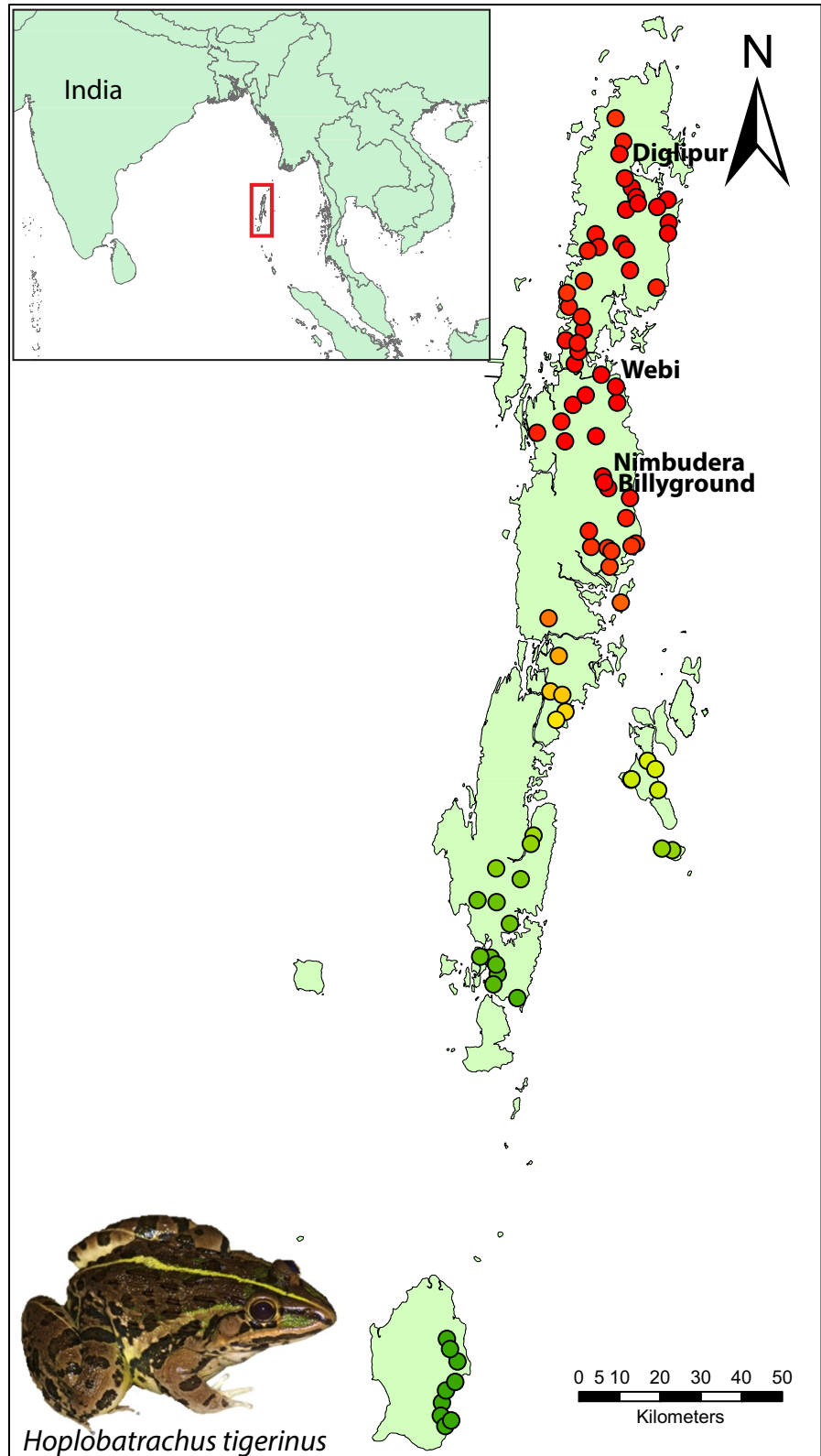
on poultry and aquaculture fish (though water contamination was reported once). Predation on centipedes (*Scolopendra* spp.), snakes, and crop pests was cited as a benefit. Of the 510 respondents we questioned on whether they consumed the bullfrog, 82.7% said no, 15.8% said yes, and 1.4% did not answer; most of those who reportedly consumed the bullfrog were concentrated in Middle Andaman. On the question of whether the respondent culled the bullfrog ( $n = 477$ ), 66.8% said no, 32.8% said yes, and 1.3% did not answer.

## Discussion

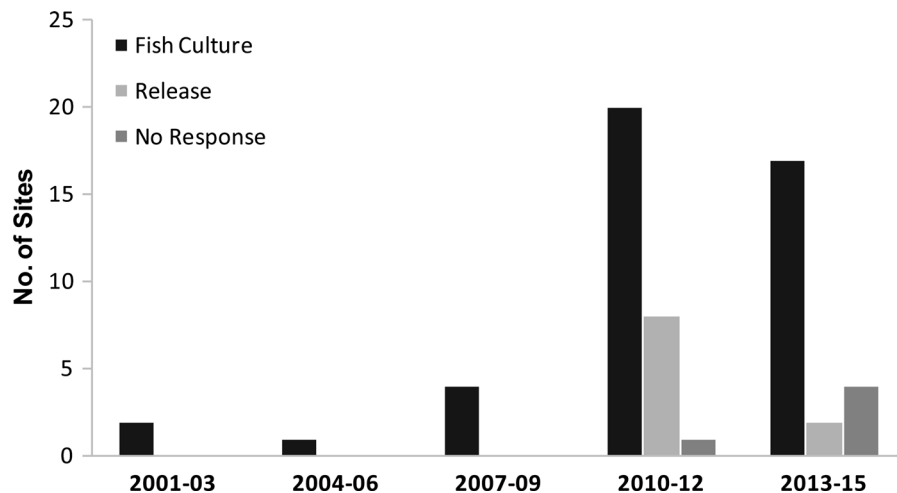
We found our novel approach to reconstruct invasion history to be effective in the case of the Indian bullfrog’s invasion on the Andaman Islands. Our approach helps define the processes underlying introduction (introduction pathways) and the expansion

phases (specific dispersal pathways and hubs), which are rarely documented (Puth and Post 2005). The approach enabled us to estimate the current distribution of the invasive bullfrog based on both key informant and visual encounter surveys (Fig. 1), to reconstruct the spread of the bullfrog over five time periods (Fig. 2) and describe dispersal pathways (Fig. 3) using key informant surveys, and finally corroborate the significance of ‘dispersal hubs’ in facilitating the invasion (Table 2; Fig. 1) by integrating spatial information from the key informant data into occupancy models. The reconstruction provides insights into the multi-faceted nature of spread in the early stages through human aided dispersal. This approach also circumvents the scarcity of museum records and publications, which may be the case with relatively new invasions or as a result of taxonomic and geographic biases in invasion science (Pyšek et al. 2008).

**Fig. 1** Site-specific occupancy estimates of the invasive Indian bullfrog *Hoplobatrachus tigerinus* at 91 villages on the Andaman archipelago. Colour gradient (green to red) denotes the occupancy estimates ranging from 0 to 1. Best predictor of occupancy is distance to nearest 'dispersal hub', defined as sites acting as sources for multiple transfers within the archipelago (labelled)







**Fig. 2** Number of villages with established populations of the Indian bullfrog *Hoplobatrachus tigerinus* on the Andaman Islands across five time periods (from 2001 to 2015), as reported by key informants. Columns for each time period separated

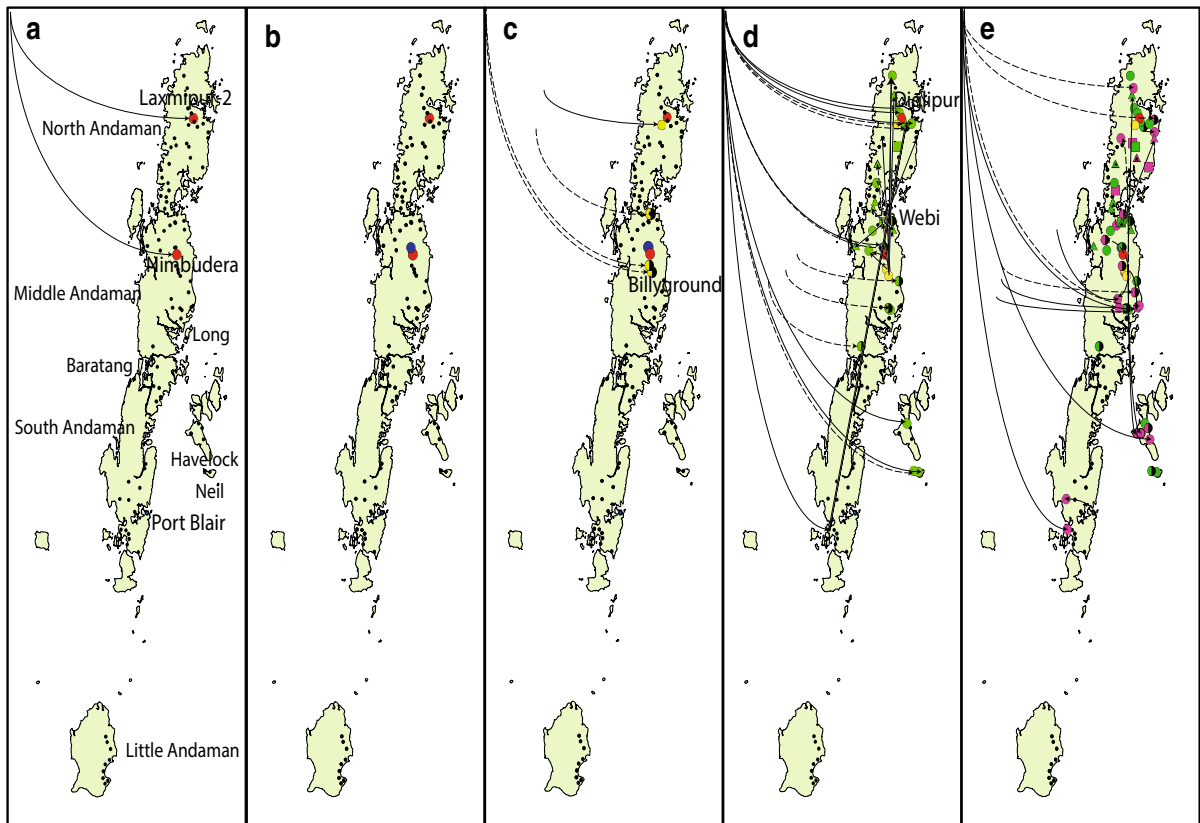
based on the reported dispersal pathway—pre-metamorphic bullfrogs as contaminant of fish culture ('fish culture'), post-metamorphic bullfrogs capture-released ('release'), and sites with no responses on dispersal

The overall occupancy rate of 0.63 (0.52–0.72), obtained from the false-positive occupancy model (Table 2) is highly similar to field survey data which find the bullfrog to occur in at least 62% of the sampled villages spread over six islands. This is a dramatic increase on the previously known invaded range (reported only in Harikrishnan and Vasudevan 2013; Rangaswamy et al. 2014) and is due to the fact that the previous studies were broad herpetofaunal assessments, focussing mostly on forested areas, whereas we specifically chose human modified areas based on existing literature describing the synanthropic nature of the species (Daniels 2005). However, invasive populations may occupy a broader niche as compared to their native range (Pearman et al. 2008) and the occurrence of the bullfrog in primary and secondary forests still needs to be assessed. The observations of a few individuals along forest streams (Harikrishnan and Vasudevan 2013) must also be validated.

The low probability of false positive detections at 4% (2–8%; Table 2) indicates the suitability of the selected participants (Mohanty et al. 2018). The bullfrog's distinctly large size as compared to native amphibians (three to five times larger), its use of human modified habitats and interactions with the public (positive and negative) is likely to positively influence the accuracy of identifications (Mohanty et al. 2018). It is important to note that high

identification accuracy may not always be the case; Somaweera et al. (2010) found that 20.5% of the general public failed to distinguish between invasive cane toad (*Rhinella marina*) and native frogs in Australia. Identification was more accurate in the case of adult males, when the respondent lived in areas invaded by the cane toad or the respondent had prior training (Somaweera et al. 2010). Therefore, the suitability of respondents, preferably key informants who are most likely to encounter the species, must be validated. It is not necessary for the invasive species in question to be restricted to human modified areas, as selection of appropriate respondents can address the issue of sampling coverage (e.g. wildlife personnel, Pillay et al. 2014).

We reconstructed the time of establishment of the bullfrog at each site using the data obtained with the public surveys. A critical issue to consider while undertaking such surveys is recall bias, which could arise out of a combination of cognitive processes (Connelly et al. 2000; Beaman et al. 2005). The longer back in time a respondent is asked to recall events, the greater the chances of inaccuracy (Coughlin 1990). Additionally, dramatic events (such as the December 2004 tsunami that had great impact in the region) may alter recall patterns and lead people to gravitate towards such events. We addressed the issue of accuracy by making our comparison categories broad (of 3 years instead of one). Though we encouraged



**Fig. 3** Villages with established populations of the Indian bullfrog *Hoplobatrachus tigerinus* on the Andaman Islands, as reported by key informants, in **a** 2001–2003, **b** 2004–2006, **c** 2007–2009, **d** 2010–2012, and **e** 2013–2015. Coloured symbols indicate new populations reported in each time period, with colours of each time period being fixed in the following periods. Circles denote fish culture as the most reported pathway, triangles denote release, and squares denote no response. Half-filled symbols indicate uncertainty in dispersal

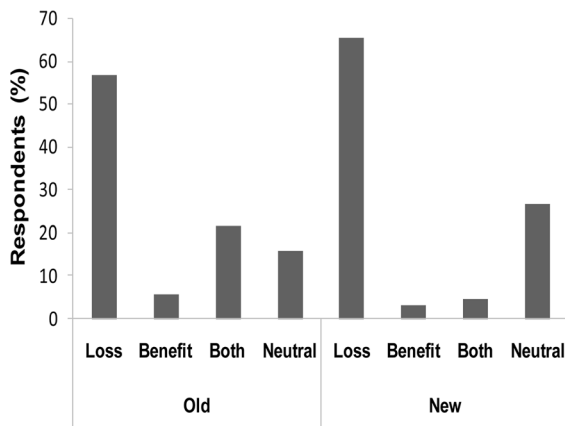
information (less than 50% responses). The direction of introduction and dispersal pathways is marked with arc line (fish culture) and straight line (release), where dotted lines indicate uncertainty in source. Arc lines with from the top-left corners represent West Bengal, India as the source and lines with uncertain origins indicate unknown location on the Indian mainland as the source. Dispersal hubs, sites which serve as origins for multiple dispersals, are labelled as Diglipur, Webi, and Billyground-Nimbudera

people to assign a year or period (instead of stating how many years ago) to their first observation of the bullfrog, we had no control over the potential tendency to gravitate towards the tsunami as a temporal reference. However, we find no evidence of distortion of recall by the tsunami, probably because the invasion occurred in most sites only after 2009. It is important to assess the applicability of our approach in moderately old invasions (up to one human generation) and address recall bias.

The invasion of the bullfrog on the Andaman Islands displays a lag phase (2000–2009) followed by an exponential expansion phase after 2009, a curve typical of biological invasions (Van Wilgen et al. 2014). It is noteworthy that the first published record

of the bullfrog on the Andaman Islands was in 2013 (by the time 40% of the sites were invaded; Harikrishnan and Vasudevan 2013), even though the local community was aware of it much earlier. Similar observations have been made in the case of invasions elsewhere (Wells 1974), and indicate the difficulty of directly studying invasions in the early stages (Hyn-dman et al. 2015).

Unintentional human-mediated dispersal of amphibians is common (García-Díaz and Cassey 2014) and can accelerate invasions (Kraus and Campbell 2002). The role of the fish culture pathway (a known pathway in amphibian invasions; Christy et al. 2007) in the introduction and post-introduction dispersal of the bullfrog is plausible given the



**Fig. 4** Perceptions of key informants on benefit and/or negative impacts incurred due to the Indian bullfrog *Hoplobatrachus tigerinus*, in sites with established bullfrog populations up until 2009 (old) and after (new)

widespread practice of fish culture for commercial and sustenance purposes in the Islands, and that the identified dispersal hubs export fish fingerling stocks. However, we do not have direct evidence of contamination and cannot confirm the reported spatio-temporal prevalence of the fish culture pathway. This purported fish culture pathway is associated with uncertainty, since it is based on respondents' interpretation of appearance of the bullfrog at a site in conjunction with low fish turnover per unit fingerling stock released. Such a perception could be a 'shared narrative' (Middleton 2012) across the Islands, though it is unlikely to operate at the large extent over which we carried out the study.

The deliberate release for consumption and novelty is known to operate frequently as a pathway in amphibian invasions (Kaiser et al. 2002; Measey et al. 2017), and vertebrate invasions in general (Hulme 2009). Similar to our findings, Ficetola et al. (2007) describe the significant role of 'personal initiatives' in the invasion of the American bullfrog (*Lithobates catesbeianus*) in Europe. Such intentional releases can move individuals over long distances (Ficetola et al. 2007; Nunes et al. 2015) and increase the likelihood of establishment (Liu et al. 2012).

Overall, the combination of these two pathways occurring frequently is likely to have resulted in the initial spread (2001–2009), where after a few sites served as dispersal hubs for new introductions triggering the exponential expansion phase. The role of dispersal hubs is particularly likely upon considering

the parallel evidence from respondents and occupancy analysis. Floerl et al. (2009) theoretically demonstrated the importance of such 'hubs' in rapidly propagating invasions to secondary sites. Lakes serving as hubs for non-native zooplankton and zebra mussel invasion to secondary lakes and streams have been identified to inform better management (Kraft et al. 2002; Muirhead and MacIsaac 2005). The chosen best model (Table 2) suggests that villages which were closer to any one of the three dispersal hubs were more likely to have the bullfrog than villages farther away (e.g. South Andaman and Little Andaman). Further, the models which specified a dispersal hub performed better than the models representing other common pathways such as *stowaway* and *unaided* dispersal due to trade and habitat disturbance. The future of the currently unmanaged invasion may depend on new dispersal hubs for the hitherto uninhabited sites (Murray et al. 2015) on Baratang, South Andaman, and the Nicobar archipelago and on the recently invaded Little Andaman Island (ca. 2018). South Andaman has only one site with confirmed bullfrog presence (Wandoor), which may serve as a source for the release pathway, but not for the fish culture pathway given that no commercial aquaculture is practised in the village.

Though leading-edge dispersal may occur between sites, alone it does not explain the spread across multiple islands (Liu et al. 2014), the short lag phase, and the continuing exponential expansion phase (Suarez et al. 2001). Under a scenario of only natural dispersal, assuming that salt water barriers between islands are overcome (e.g. by vegetation rafts; Bell et al. 2015), the origin point in new islands should be closest to the nearest point across the barrier. However, the observed pattern of spread does not support this notion (Fig. 3). Further, the recorded release events moved the bullfrog over long distances (48 km on an average), some of which may have resulted in establishment. We infer that multiple human mediated jump dispersals, both intentional and accidental, have occurred (and probably continue to occur) within and between islands, possibly combined with an active pathway (fish culture) between the Indian mainland and the Andaman Islands. The influence of human mediated dispersal is particularly strong in the case of herpetofauna in archipelagos, where natural salt water barriers are frequently breached by human assistance (Liu et al. 2014).

The reported negative perception of the bullfrog among the majority of the respondents reflects apprehensions of its negative impact on two household level economies, aquaculture and poultry. This potential impact must be quantified and considered while assessing the overall economic impact of the species (Bacher et al. 2017). The stated reasons for benefit (pest control) and negative impact (threat to economy) are not unfounded, as there are records of the bullfrog preying on fish, poultry, crop pests, and scolopendrian centipedes in the region (Mohanty and Measey 2018). Voluntary culling of the bullfrog by private citizens reflect the perceived negative impact (as with *Rhinella marina*, Somaweera et al. 2010), whereas the geographic concentration in consumption pattern may be due to local cultural factors.

## Conclusion

Biological invasions, by definition, encompass humans as a key component. Yet the potential of using human knowledge to aid in reconstruction of invasions has been underappreciated. We show the utility of public surveys in identifying pathways, dispersal hubs, and understanding spatio-temporal changes in invasive spread. In addition, such surveys provide an opportunity to assess economic impacts and human perceptions for impact assessments (Bacher et al. 2017). We believe that our approach is scalable to other systems and species, as long as the subject is easily identified by the public (or a subset of key informants) and the invasion being reconstructed is relatively recent.

**Acknowledgements** This research was supported by the DST-NRF Centre of Excellence for Invasion Biology (CIB) and approved by the Human Research (Humanities) Ethics committee of Stellenbosch University (SU-HSD-003771). We would like to thank, the Department of Environment and Forests, Andaman and Nicobar Islands for Granting permits (#CWLW/WL/134/350); the Inlaks Shivdasani Foundation-Ravi Sankaran Fellowship Programme, the Rufford Small Grants (#20818-2) for funding and the Department of Botany and Zoology, Stellenbosch University for a bursary to NPM; the Andaman & Nicobar Environment Team (ANET) for facilitating field work; all the respondents for contributing to our understanding of the subject; Sachin Anand, Saw Isaac, Bipin Tirkey for collecting part of the data, and Suresh Kujur for help during field work; Prof. David M Richardson, Dr. Ana Novoa, Susan Canavan, and Sahir Advani for feedback on the manuscript; Dr. Kevin Smith and two anonymous referees for

constructive criticism which improved the manuscript. NPM would like to acknowledge the support and advice of Dr. Karthikeyan Vasudevan, Dr. Manish Chandi, and Harikrishnan S. during the study.

**Author contributions** NPM and JM conceived the idea of the study; NPM collected the data; NPM and JM analysed the data; NPM wrote the manuscript, JM contributed to the writing.

**Data availability statement** The data used in this paper has been submitted to a standard data repository (<http://www.datadryad.org/>).

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